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Pollen morphology of some members of Piperaceae and its bearing on the systematics and phylogeny of the family

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Abstract

Pollen morphology of 17 species of *Piper*, 8 cultivars of *Piper nigrum*, 13 species of *Peperomia* and the monotypic genus *Heckeria* of the family Piperaceae from South India was studied by both light and scanning electron microscopy. Two pollen types could be recognized : (1) Piper type (*Piper*, *Heckeria*) with isobilateral, monocolpate grains showing predominantly echinate exine surface pattern, and (2) Peperomia type (*Peperomia*) with radiosymmetric inaperturate grains showing predominantly areolate-spinulate exine. The pollen grains of all the three genera are very small-sized. Pollen features are shown to support closer affinity of the Piperaceae with Saururaceae. This also favours more evolved status of the *Piper* group than *Peperomia* within the family. The difference in the pollen features of *Peperomia* with the remainder of Piperaceae supports its segregation into a separate family Peperomiaceae.

INTRODUCTION

The Piperaceae are a large family comprising over 3000 species in 9 genera (Kupicha, 1993), of which *Piper* L. and *Peperomia* Ruiz & Pav. are the major ones, whose chief centres are Central and South America (Trelease & Yuncker, 1950). Their world distribution has been divided into 12 major centres (Datta & Dasgupta, 1977), one of which is the Indian subcontinent. In the Indian region, two independent centres of distribution have been recognized, namely the Trans-gangetic North–Eastern region and the South Deccan (Rahiman, 1987). Hooker (1886) described 56 species in 3 genera, viz., *Piper*, *Peperomia* and *Houttuynia* from the Indian subcontinent and Gamble (1925) recorded 13 species of *Piper*, 6 species of *Peperomia* and one in the monotypic genus *Heckeria* from South India. The family includes a number of economically and medicinally important species, of which *Piper nigrum* L. is the most important, which yields the 'Black pepper' of commerce, known as the 'King of Spices' a

highly valued condiment used as a culinary spice world over. Many species of *Peperomia* are favoured garden plants grown for their ornamental foliage.

Taxonomically the family is known to be a very puzzling group. Although palynological data have been recognized as a potential supplementary tool for tackling taxonomic and phylogenetic problems of related plant groups (Nair, 1974), palynological information on the Piperaceae is very scanty in general, and that too only on a handful of alien taxa (Erdtman, 1952; Smith, 1975). The South Indian group is almost unexplored. The present study concerns LM and SEM results of 17 species of *Piper*, 8 cultivars of *P.nigrum*, 13 species of *Peperomia* and one of *Heckeria* from South India, of which 4 species of *Piper* and 6 species of *Peperomia* are well established exotics grown as introduced plants in the region. The results of the study are discussed in relation to the systematics and phylogeny of the family.

MATERIALS AND METHODS

The polleniferous materials were collected from live plants from different localities of their distribution in South India. In the case of exotic species (*Piper arboreum*, *P. betle*, *P. colubrinum*, *P. magnificum*, *Peperomia clusiifolia*, *P. incana*, *P. obtusifolia*, *P. polybotrya*, *P. sandersii*, *P. scandens*) the materials used were from plants grown in the Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram. Anthers from mature flowers were fixed in glacial acetic acid. Pollen preparations were made by acetolysis method (Erdtman, 1952) for LM study. For SEM study, the grains were stored in ethanol, coated with gold and scanned at the National Botanical Research Institute, Lucknow. Pollen terminology follows Erdtman (1967), and the pollen shape classes were determined after Walker and Doyle (1975). Pollen measurements were based on a sample size of 100 grains of each taxon. Voucher specimens of the taxa studied (Table 1) are deposited at the Herbarium of the Tropical Botanic Garden and Research Institute (TBGT), Palode, Thiruvananthapuram.

Table 1. List of taxa studied and their sources

Name of taxa	Voucher specimen No.	Locality/ Source	District & State
1	2	3	4
***Piper* L.**			
P. galeatum C.DC.	19475	Munnar	Idukki, K
P. trichostachyon C.DC.	19426	Neymacadu	Idukki, K
P. longum L.	5848	Thenmala	Thiruvananthapuram, K
P. hapnium Buch. - Ham	19407	Palode	Thiruvananthapuram, K
P. brachystachum Wall.	8806	Kakki	Pathanamthitta, K
P. hookeri Miq.	8807	Kodaikanal	Anna, TN

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1	2	3	4
P. schmidtii Hook.f.	8823	Avalanchi	Udagamandalam, TN
P. barberi Gamble	5699	Changili	Thiruvananthapuram, K
P. nigrum L. (cultivars)			
'Ampirian'	25333	Palode	Thiruvananthapuram, K
'Cherumany'	25315	Naiketty	Wayanad, K
'Kanjiramkodan'	25312	Kalpetta	Wayanad, K
'Karimunda'	12906	Peruvanthanam	Idukki, K
'Karimundy'	22621	Pulpally	Wayanad, K
'Kottanadan'	7737	Peringamala	Thiruvananthapuram, K
'Panickaruvally'	25314	Naiketty	Wayanad, K
'Peringamala'	25346	Peringamala	Thiruvananthapuram, K
P. hymenophyllum Miq.	7280	Pamba	Pathanamthitta, K
P. argyrophyllum Miq.	5023	Lower Kodayar	Tirunelveli, TN
P. attenuatum Miq.	2722	Athirapally	Trichur, K
P. wightii Miq.	8807	Agastymala	Thiruvananthapuram, K
P. arboreum Aubl.#	19454	TBGRI*	Thiruvananthapuram, K
P. betle L.#	19460	IIHR*	Bangalore, KA
P. colubrinum Link.#	12186	IISR*	Kozhikode, K
P. magnificum Trel.#	887	TBGRI	Thiruvananthapuram, K
Heckeria Kunth			
H. subpeltata Kunth#	13009	Palaruvi	Kollam, K
Peperomia Ruiz & Pav.			
P. reflexa A. Dietr.	12163	Athirumala	Thiruvananthapuram, K
P. heyneana Miq.	8831	Upper Kodayar	Thirunelveli, TN
P. thomsoni Hook.f.	19463	Ponmudi	Thiruvananthapuram, K
P. portulacoides A. Dietr.	12110	Peerumedu	Idukki, K
P. wightiana Miq.	19449	Periya	Wayanad, K
P. dindigulensis Miq.	12193	Adivaram	Kozhikode, K
P. pellucida H.B. & K.#	19470	TBGRI	Trivandrum, K
P. clusiifolia (Jacq.) Hook.#	12190	NGBS*	Wayanad, K
P. incana A. Dietr.	885	NGBS	Wayanadu, K

1	2	3	4
P. obtusifolia C.DC.#	19477	NGBS	Wayanad, K
P. polybotrya H.B. & K.#	19478	NGBS	Wayanad, K
P. sandersii C.DC. #	886	NGBS	Wayanad, K
P. scandens Ruiz. & Pav.#	19191	NGBS	Wayanad, K

Exotic species

*TBGRI – Tropical Botanic Garden & Research Institute; *IIHR – Indian Institute of Horticultural Research; *IISR – Indian Institute of Spices Research; *NGBS– Narayana Gurukula Botanical Sanctuary; K – Kerala; KA – Karnataka; TN – Tamil Nadu.

RESULTS

The important pollen morphological features observed in species of *Piper*, *Peperomia* and *Heckeria* are summarized in Table 2. SEM pictures of the pollen of some species of *Piper* (Fig. 1: a-f; Fig. 2: g-l) and *Peperomia* (Fig. 3: m-r) are provided.

The pollen grains of all the species of *Piper*, and *Heckeria subpeltata* were consistently isobilateral and monocolpate with the aperture in the zonal position. The colpus furrow was narrow and long with tapering ends, almost extending to the poles in most species of *Piper*. However, in a few, the colpi were wider and shorter, and in certain cases (*P. schmidtii*) the ends of the colpus were broad and wide. All the species of *Peperomia* had radiosymmetric and inaperturate grains. The pollen grains of species of all the three genera were very small-sized, in general ranging from 6.2 x 6.0 µm – 9.0 x 6.66 µm; and in a few polyploid species of both *Piper* and *Peperomia* the grains were slightly larger; up to 11.3 x 9.8 µm in *Piper* (*P. brachystachyum*) and 13.2 x 10.4 µm in *Peperomia* (*P. portulacoides*). In one of the species of *Piper* (*P. galeatum*) the grains were extremely small sized (3.8 x 3.4 µm). The pollen shape-types noticed were spheroidal, prolate-spheroidal and subprolate in species of both *Piper* and *Peteromia*, and prolate-spheroidal in *Heckeria*. The predominant shape-type in *Piper* was prolate-spheroidal, while in *Peperomia* spheroidal. The exine surface patterns noticed in species of *Piper* were rugulate, verrucate, plated-spinulate or echinate, of which the echinate predominated. The surface in some of the species (see a, b - f in Fig.1 and i - l in Fig. 2) showed island / plate formations of various sizes and shapes. The surface in them is plated - spinulate, the plates being either at one level (layer) or at 2 or more levels (layers) superimposed over each other. Echinate condition is seen in 'b' and 'c' and in others spinulate . In *Peperomia* the most frequent type was the spinulate pattern, and in addition psilate, rugulate and echinate conditions were exhibited by one species each. In the species with spinulate pattern the spinules were seen to be located on differently sized and shaped areoles. The number of spinules per areole in different species showed wide variation (3-20); the highest number per areole was in *Peperomia dindigulensis* (14-20) followed by *P. polybotrya* (10-17),

and the lowest in *P. sandersii* (3-5). The projections are fundamentally tuberculate (m-o in Fig. 3) the tubercles being adpressed making a negative reticulum. The tubercles are free as in 'n' and adnate-tuberculate as in 'r' in Fig.3. The pollen shape in the species of *Heckeria* was prolate-spheroidal, and its exine surface was echinate.

Table 2. Important palynological features of species of the Piperaceae

Name of taxa	Aperture	Pollen shape	Pollen size (μm)	Exine ornamentation
1	2	3	4	5
Piper				
P.galeatum	monocolpate	prolate – spheroidal	3.8 x 3.4	verrucate
P.trichostachyon	monocolpate	subprolate	8.4 x 6.4	spinulate
P.longum	monocolpate	prolate – spheroidal	8.1 x 6.9	spinulate
P.hapnium	monocolpate	prolate – spheroidal	7.5 x 6.5	spinulate
P.brachystachyum	monocolpate	subprolate	11.3 x 9.8	spinulate
P.hookeri	monocolpate	subprolate	7.1 x 6.9	granulate-rugulate
P. schmidtii	monocolpate	subprolate	7.3 x 5.9	spinulate
P. barberi	monocolpate	subprolate	8.3 x 6.3	echinate
P. nigrum (cultivars)				
'Ampirian'	monocolpate	subprolate	7.6 x 5.3	echinate
'Cherumany'	monocolpate	prolate – spheroidal	8.0 x 7.0	echinate
'Kanjiramkodan'	monocolpate	subprolate	6.8 x 5.4	areolate-spinulate
'Karimunda'	monocolpate	subprolate	7.6 x 5.4	echinate
'Karimundy'	monocolpate	spheroidal	6.2 x 6.0	echinate
'Kottanadan'	monocolpate	prolate – spheroidal	8.1 x 7.4	echinate
'Panickaruvally'	monocolpate	prolate – spheroidal	7.6 x 6.8	echinate
'Peringamala'	monocolpate	spheroidal	7.0 x 6.8	echinate
P. hymenophyllum	monocolpate	subprolate	7.8 x 6.5	echinate
P. argyrophyllum	monocolpate	prolate – spheroidal	7.2 x 6.8	echinate
P. attenuatum	monocolpate	prolate – spheroidal	10.0 x 9.0	echinate
P. wightii	monocolpate	subprolate	10.0 x 8.1	spinulate
P. arboreum	monocolpate	spheroidal	10.1 x 9.9	spinulate

1	2	3	4	5
P. betle	monocolpate	subprolate	7.3 x 5.4	echinate
P. colubrinum	monocolpate	prolate – spheroidal	9.0 x 6.6	spinulate
P .magnificum	monocolpate	subprolate	7.1 x 6.1	spinulate
Heckeria				
H.subpeltata	monocolpate	prolate-spheroidal	8.3 x 7.0	echinate
Peperomia				
P. reflexa	inaperturate	prolate-spheroidal	8.0 x 7.0	spinulate
P. heyneana	inaperturate	subprolate	7.6 x 6.0	areolate-spinulate
P. thomsoni	inaperturate	prolate-spheroidal	11.6 x 10.8	rugulate-perforate
P. portulacoides	inaperturate	subprolate	13.2 x 10.4	psilate
P. wightiana	inaperturate	prolate-spheroidal	7.2 x 6.8	areolate-spinulate
P. dindigulensis	inaperturate	prolate-spheroidal	8.3 x 7.8	areolate-spinulate
P. pellucida	inaperturate	prolate-spheroidal	8.9 x 8.0	areolate-spinulate
P. clusifolia	inaperturate	spheroidal	7.0 x 6.8	areolate-spinulate
P. incana	inaperturate	spheroidal	9.2 x 8.8	areolate-spinulate
P. obtusifolia	inaperturate	spheroidal	7.0 x 6.8	areolate-spinulate
P. polybotrya	inaperturate	spheroidal	6.8 x 6.7	areolate-spinulate
P. sandersii	inaperturate	prolate-spheroidal	7.0 x 6.4	areolate-spinulate
P. scandens	inaperturate	spheroidal	9.0 x 8.8	areolate-spinulate

DISCUSSION

Generally the cause of morphological evolution of pollen are assessed based on the position of the aperture, their number and form. Proximal, distal, zonal and global are considered to be the hierarchical order of evolutionary progress (Nair, 1974), of which the zonal and global are restricted to Angiosperms. Among the present taxa, members of the genus *Piper* and *Heckeria*, have their aperture in the zonal position. The number and distribution of the aperture forms are among the many trends in the evolution of pollen morphology (Walker & Doyle, 1975; Van Campo, 1976). An evolutionary sequence from simple to more complex apertural types has generally been contemplated (Chanda *et al.*, 1979), and increase in number from primitive to advanced appears to be the general trend. The pollen grains of monocots have one aperture and those of dicots usually three. The inaperturate (omniaperturate) condition occurs in the most primitive monocots (Helobiae) and primitive dicots (Polycarpae). In the present group, all the species of *Peperomia* are inaperturate and this is strikingly in contrast with the situation in the other two genera of the family, *Piper* and *Heckeria* in which the grains are consistently aperturate (monocolpate). As regards the size of the colpi, some degree of difference is apparent in *Piper*; some having long and narrow furrows with tapering ends and in others shorter and wider with round or broad colpus ends. Majority of the primitive families of the Ranalian complex, including the Saururaceae and Piperaceae are reported to show psilate exine sculpturing (cf. Walker, 1973) with scabrate, verrucate and echinate in addition. Among the present taxa of the family the most frequent exine surface pattern is echinate in *Piper* and also in *Heckeria*, while in *Peperomia* this is mostly spinulate.

The shape of pollen is usually unfixed in angiosperms, and hence this character has not been considered as a reliable parameter in pollen morphological analysis in relation to taxonomy and phylogeny. Judged by the P/E ratio, several shape classes are recognized in angiosperms (Walker & Doyle, 1975), of which the spheroidal is considered to be the most basic type, which changes in either direction. In the present group the shape categories noticed are spheroidal, prolate–spheroidal and subprolate, of which the proalte-spheroidal dominates in *Piper* and spheroidal in *Peperomia*. Pollen size is usually considered to be of less diagnostic value, but this character has been shown to be useful in cytopalynological studies (Bir & Sidhu, 1980; Nair & Ravikumar, 1984; Saraswathyamma *et al.*, 1995; Meenakumari *et al.*, 1996) in as much as the information on pollen size having provided an index to chromosome numerical variations. In the three Piperaceous genera studied here, the pollen grains are very small with size ranging from 6.2 x 6.0 – 11.3 x 9.8 µm in *Piper* and 6.8 x 6.7 - 13.2 x 10.4 µm in *Peperomia*. Although some of the polyploid taxa in both *Piper* and *Peperomia* such as the (x=16) *Piper brachystachyum* (Mathew *et al* 1998 a) and (x=4) *Peperomia portulacoides* (Mathew *et al.*, 1998b) showed larger pollen size in relation to ploidy levels in both genera, there was no consistent positive correlation between pollen size and ploidy status.

In the light of the palynological data presented here on the South Indian members of the Piperaceae it may be possible to figure out two distinct pollen types viz., Piper type and Peperomia type in the family with the charactersitics as shown below:

Pollen feature	Piper type *(Piper, Heckeria)*	Peperomia type *(Peperomia)*
a) Pollen symmetry	Isobilateral	Radiosymmetric
b) Pollen class	Monocolpate	Inaperturate
c) Exine surface	Predominantly echinate	Predominantly areolate-spinulate
d) Pollen shape	Predominantly prolate-spheroidal	Predominantly spheroidal

Pollen morphological data have been used in many studies related to cultivar taxonomy, and it has been demonstrated that statistical analysis of pollen variations has yielded viable information in the understanding of hybridity status of cultivars in crop species (Nair, 1961). In the South Indian State of Kerala there are a number of established and distinct varieties of *P. nigrum* under cultivation, of which pollen morphology of eight cultivars has been studied here. All the eight cultivars are similar in the basic aperture character (monocolpate), and their pollen size is also comparable. However, some difference was apparent in respect of the other features like pollen shape (spheroidal, prolate-spheroidal, subprolate). It is expected that a study of more cultivars of the species of the region, which is in progress, may yield meaningful data in relation to intraspecific taxonomy of this valuable crop species. Taxonomists are very much disagreed on many aspects of the systematics of the family, and there exists great confusion concerning the composition, interrelationships and affinities in the different classificatory treatments, both classical and modern. The family is considered to be a taxonomically difficult group (Burger, 1972) and is one of the most messes in plant taxonomy (Howard, 1973).

The members exhibit a number of anomalies, which puzzle any interpretation of plausible phylogenetic sequence. An important anatomical feature is that concerning the vascular bundles in two or more circles with the outer ones united or scattered as in monocots. This has prompted some of the early botanists to place it near the Araceae. The family also displays a suite of features, which are uncommon among dicots (Burger, 1977). But, unlike the monocots, the stem grows in thickness by cambial activity, which is a dicot feature (Metcalfe & Chalk, 1950). Yuncker (1958) has held that embryonic and other features of dicot nature evident in the group more than offset the suspected monocot alliance. A significant attribute in relation to the phylogenetic position of the family is the simplicity of the floral structure. Whether the Piperaceous flower is to be reckoned as primitive or advanced is again a question on which there is no general concord. Concerning the affinities of the Piperaceae, there has been no agreement among taxonomists. Although affinity has been suggested with a number of primitive dicot families, most taxonomic treatments ascribe closer affinity with the Saururaceae (Bentham & Hooker, 1880; Johnson, 1902; Bessey, 1915; Skottsberg, 1946; Hutchinson, 1959; Thorne, 1976; Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981; Bedell & Reveal, 1982). Palynological semblance between the members of Saururaceae and *Piper* – the type genus of the Piperaceae (Walker, 1973) (very small, isobilateral, monocolpate grains with psilate, verrucate and echinate exine surface pattern) offer conceivable support to this affinity.

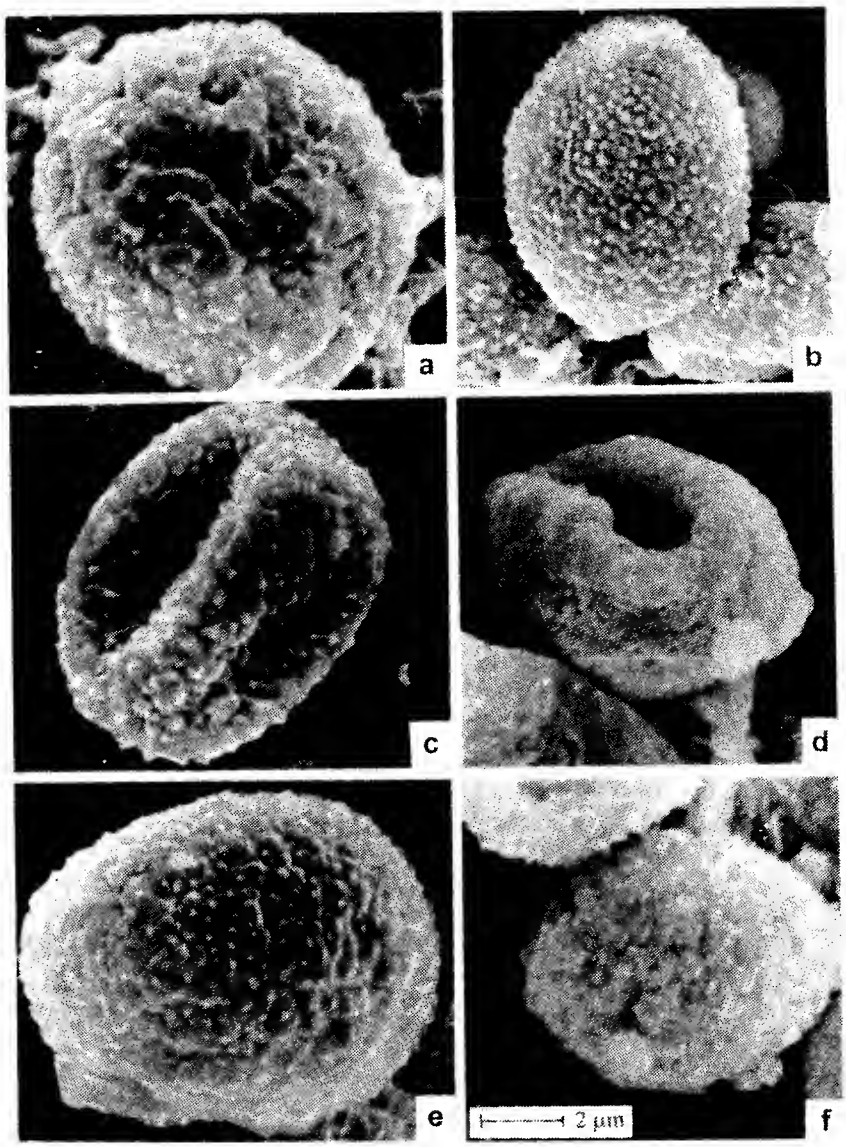

Fig. 1. Scanning electron micrographs of pollen grains of species of *Piper*: a. *P. arboreum* – exine spinulate; b. *P. betle* – exine echinate; c. *P. barberi* – exine echinate; d. *P. colubrinum*, exine spinulate; e. *P. brachystachyum* – exine spinulate; f. *P. hapnium* – exine spinulate.

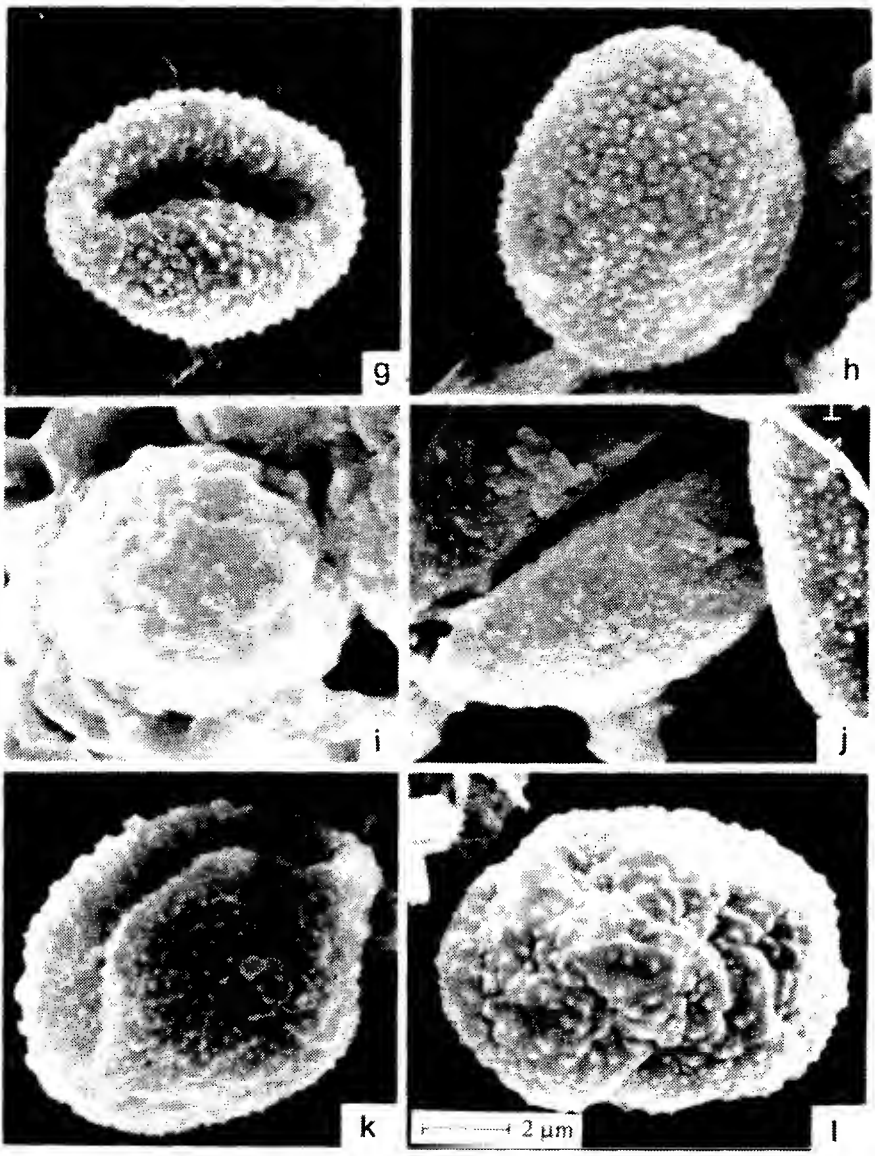

Fig. 2. Scanning electron micrographs of pollen grains of species of *Piper*: g. *P. schmidtii* – exine spinulate; h. *P. longum* – exine spinulate; i. *P. nigrum* 'Kanjiramkodan' – exine areolate spinulate; j. *P. magnificum* – exine spinulate; k. *P. trichostachyon* – exine spinulate; l. *P. wightii* – exine spinulate.

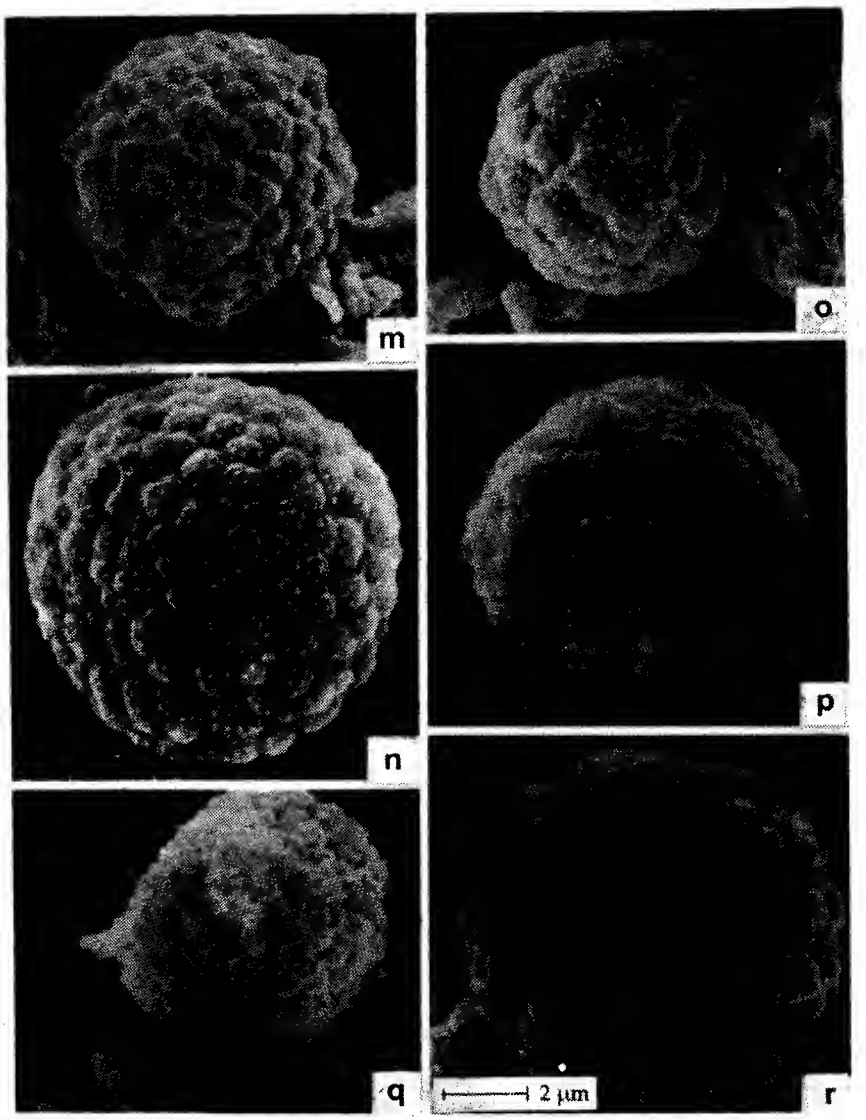

Fig. 3. Scanning electron micrographs of pollen grains of species of *Peperomia*: m. *P. clusiifolia* – exine areolate-spinulate with 4-6 spinules per areole; n. *P. incana* – exine areolate-spinulate with 7-12 spinules per areole; o. *P. polybotrya* – exine areolate-spinulate with 10-17 spinules per areole; p. *P. reflexa* – exine spinulate; q. *P. sandersii* - exine areolate-spinulate with 3-5 spinules per areole; r. *P. scandens* – exine areolate-spinulate with 5-7 spinules per areole.

The question of relative phylogenetic position of the two major genera, *Piper* and *Peperomia* within the family has been variously interpreted. The *Peperomia* group has been generally considered to be the more evolved and advanced for its herbaceous habit and more reduced floral structure. But, palynological features appear to subscribe more towards the view that the *Piper* group could be the more evolved in the family than *Peperomia* in as much as the former is endowed with aperturate (monocolpate) pollen grains with predominanlty echinate exine surface as against the more primitive inaperturate grains with areolate-spinulate exine in *Peperomia*. The chromosomal features exhibited by the two genera also favour this possibility on the ground that the karyotypes of the species of *Piper* are consistently specialized with very small-sized chromosomes (Mathew *et al.*, 1998a) in contrast to the unspecialized karyotype of *Peperomia* in which the chromosomes are large-sized and meta-and submetacentric (Mathew *et al.*, 1998b).

Major similarities between *Piper* and *Peperomia* rest on the pattern of distribution of vascular bundles in the stem, spike-like inflorescence, bisexual flowers lacking perianth, one-celled ovary with one ovule. But *Peperomia* is distinct from *Piper* in respect of a spectrum of character-attributes like herbaceous habit, non-sheating leaf base, lack of stipule, axillary spikes, more reduced flowers and also concerning the shape and appearance of subtending bracts (peltate-orbicular), position of stigma (eccentric), shape and size of fruit (ovoid, very small), etc. The wide exomorphic difference between the two generic groups has prompted some taxonomists to advocate segregation of the two, granting *Peperomia* the rank of a separate family, Peperomiaceae (Smith, 1972). The marked palynological distinction evident between *Piper* and *Peperomia* may be considered to offer convincing support to this proposition, which again is amply corroborated by the karyological distinction between the two genera.

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